

“The Smallest Grain in the Balance”

KENNETH M. WEISS

Darwin viewed evolution as a continuous force perfectly sensitive to variation. The nearly-neutral theory of evolution says something quite different. Both may be right.

A force is a particular kind of notion in science. It is a fundamental concept in Newtonian physics that is defined as having both strength and direction. Force is continuous and quantitative, not sporadic, probabilistic, or discretely packaged. Charles Darwin had a Newtonian view of life that still dominates in evolutionary biology. Perhaps because he drew inspiration from the uniformitarian geology then being revealed by Charles Lyell, Darwin's view of the world was one of process continuity, which he specifically opposed to the static, discrete creationism then prevailing.

The essence of Darwin's view was clear from before the *Origin of Species* was published. An advantageous trait would experience the force-like favor of selection. This is at the very Darwinian core, and throughout his life he emphatically and repeatedly opposed saltational evolution: *natura non facit saltum*—new traits do not arise by sudden leaps. Most individuals in a species are rather similar, true to their modal “type.” *Slight* advantage was the key to how these modal types evolve new adaptive function. There must have been “almost unlimited time . . . millions on millions of generations” and natural selection de-

termines even “the smallest grain in the balance” of competition that “will determine on which death shall fall, and which shall survive.” Thus the “unerring power at work in natural selection” will lead that advantageous trait to become a new adaptation.¹ Darwin concludes the *Origin* by making clear his Newtonian view of evolution as a continuous, essentially perfect Law of Nature by which species have been “produced by laws acting all around us . . . whilst this planet has gone cycling on according to the fixed law of gravity.”

In 1687, Isaac Newton began his *Principia Mathematica* by developing what we now call calculus as a way of analyzing dynamic change in a seamless universe, for which he introduced the principle of infinitesimals (Figure 1). At the time, the mathematics of science largely meant geometry and this was an awkward tool for his purpose. So Newton showed how in a geometrically described phenomenon such as a particular motion, the concept of ever-smaller intervals of one variable, like time, would cover correspondingly smaller intervals of space. Relative relationships would hold while being infinitely reduced in absolute scale. This, for example, is how we work out derivatives and integrals as limits, as the interval on one axis is gradually reduced to zero. The parameters of physics are inherent proper-

ties of objects, whose motion, and the effects of force on them, is reducibly smooth. This reflects a core conceptual axiom of much of science that the causal fabric of space and time is universal, unexceptioned, continuous, and hence infinitely divisible.

This is how Darwin viewed causation in evolution. Natural selection is a force that works on objects over time. We can represent darwinian selection conceptually as a coefficient conferring an advantage of amount s upon bearers of a favored trait (s is negative for a harmful one). s is treated as a Newtonian parameter in that no matter how small its value, it will ineluctably have its effect over “millions on millions” of generations. In a Newtonian world, long term projections can be made—“planets go on cycling . . .” Despite occasional caveats (mainly in the rarefied world of population genetics) this is still essentially how adaptive scenarios are reconstructed.

But this is not how life is! For one thing, Darwin's contemporary Gregor Mendel worked from the different perspective of chemistry that at the time was developing explanations in terms of discrete atomic units.¹ The prominent geneticist William Bateson called Mendel's experiments “worthy to rank with those which laid the foundation of the Atomic Laws of Chemistry.”² Mendel found that inheritance is discrete, and biology has become ever more molecular. Modern population genetics, the formal theory of evolution, is today largely a stochastic theory, because of particulate inheritance and because reproduction is also a discrete event in finite populations. This fundamentally changes the nature of s to a discrete, probabilistic notion, and achieved fitness is its stochastic result. When s is small—

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¹Quotes are respectively from CD's 1857 letter to Asa Gray; section of his 1844 notebook read to the Linnaean Society in 1858; the same; Gray letter.

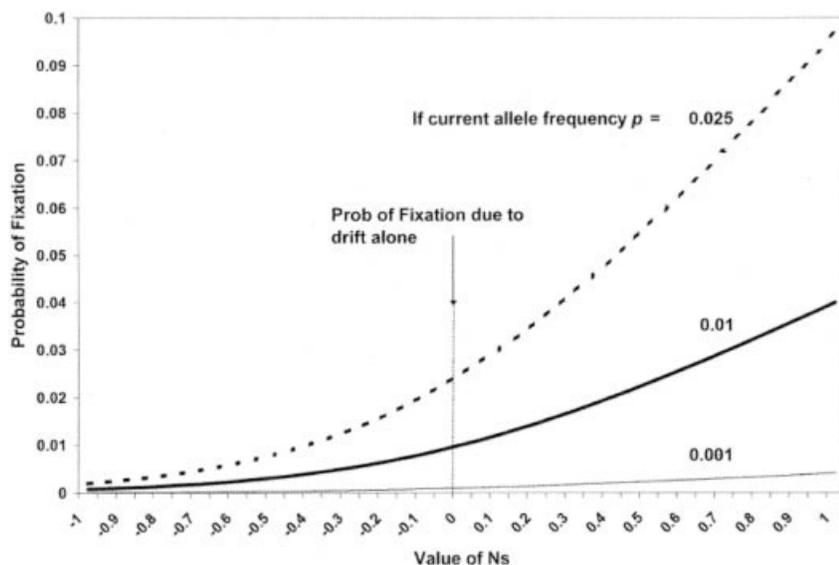


Figure 2. Small Ns means drift dominates fate of allele with current frequency = p . (bottom line is for frequency 20 times greater than that estimated for a new mutation in the ancestral human population of $N = 10^4$).

ected by layers of stochasticity. If we are uniformitarians about life we have to accept that what we see all around us today is generally how life is—and *was*. Everyday experience, about most species including ourselves and other primates, is that there is a lot of variation among those who successfully reproduce. We know that selection can be strong, and we can impose it artificially, as we do with pesticides and exuberant use of antibiotics. The main examples of strong *natural* selective forces are the serious, often congenital, harmful effects that, along with their genetic basis, are quickly weeded out by selection. But these were not of interest to Darwin for whom all monsters were hopeless.

Given what we know, if we need a slogan, one more appropriate than Survival of the Fittest, would be that selection mainly works by Failure of the Frail. Truncation of seriously defective variants is the most prevalent, least fickle, most consistent force-like effect of natural selection. The idea that selection is mainly negative was advanced even in the 19th century, but for dated reasons, and was discredited by the advancing front of directional gradualism, because the objective was to account for “positive” adaptations, not biological wreckage. A modern view of Failure of the Frail

is that, as we see all around us all the time, the relative selective coefficients of most viable individuals are nearly identical. But in light of the stochastic chaos of reproduction, that realization is actually a threat to the slow gradualism upon which Darwin insisted.

Darwin’s opposition to saltational changes forced him to grapple with the evolution of new, complex traits, like our eyes. His idea was an evolution through “graduated steps” that move piece-wise toward the present-day trait, each step adapted by selection for its own value, presumably related to (but not specifically aiming toward) the refined present-day version. A common term for this was “preadaptation” but to avoid even a hint of teleology, Gould and Vrba introduced the term “exaptation,”¹⁰ for states that evolved for some purpose unrelated to but later co-opted for the complex one we find today. We can also view Sewall Wright’s famous “adaptive landscape” (see¹¹) in a similar way. He suggested a lumpy fitness landscape, in which peaks represent states of fitness proportionate to their heights, to explain how new traits could evolve when gradual selection in very large random-mating populations might be too constraining and conservative, or might not be able to

get around lower peaks to find the highest peak. Both notions involved an important step (not leap) of chance. Exaptations were due to functional variation that only related by chance to the “final” trait we observe today (no foresight). Genetic drift in small populations could enable individuals to skip around the surface a bit, enabling them to bypass lower peaks to find higher ones. But in both views, once a population gets near these local states by chance it is then molded by gradualistic selection to reach the adaptive peak itself. These ideas modify Darwin’s Newtonian purism, and they help. But they don’t go far enough.

Figure 2 shows the theoretical probability that an allele with current frequency p will ultimately be fixed in a population (that is, will replace other existing alleles), as a function of the value of the product Ns , where N is the population size (see⁸ and my web page for references on this theory and its use).² Each curve represents the probability that an allele at a given frequency will eventually become fixed (Y axis), as a function of the product Ns (X axis). When drift alone is operating (strict selective neutrality, or $s = 0$), the chance of fixation is equal to the allele frequency itself (vertical dotted line). But if the magnitude of Ns is small, as may be typical, the probability of fixation is not much different than the chance of fixation by chance alone.

Darwin didn’t understand inheritance correctly and his smallest competitive grains referred to *traits* rather than genes. But traits, especially of the kind most important to paleontologists and evolutionary biologists, are affected by many genes, each making partial contributions. This means that the selective coefficient for any one of those genes is proportionately less than the smallest-grain advantage of the trait itself, implying an even greater role for drift at the individual gene level. By being complex, the trait itself might be more stable in its course than its contributing genes,

²More properly we use the “effective” rather than census population size, taking account of overlapping generations, local demic subdivision, etc.

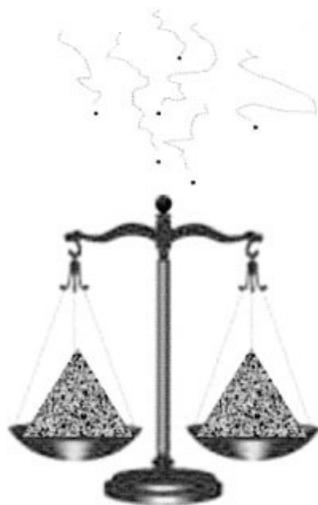


Figure 3. Where will the grains fall?

but for reasons described earlier, theoretical models of phenotypic as well as genotypic evolution show that drift can be difficult to rule out unless selection is strong, which is just what we don't need to model!

The truth is actually somewhat worse. Tomoko Ohta and others have used the general result shown in Figure 2 to suggest that, remarkably, a substantial fraction even of slightly *deleterious* mutations may become fixed because their probability of fixation roughly equals that of drift. And conversely, the chance that most slightly *advantageous* alleles will become fixed is actually very slight, even if their selective coefficient s were stable rather than probabilistic.

This was not what Darwin had in mind! In a Newtonian race, the tiniest advantage will inevitably decide "which shall live and which shall die," but for this to be so the competitors would always have to be on the razor's edge of survival so that a "smallest grain" of advantage could always be telling. But this is clearly not the general case in life, leaving us with the problem of explaining the obvious adaptive nature of nature's creatures. How could a variant with only a slight probabilistic advantage actually advance against the forces of chance? Over the years, many modifications of conventional selective arguments have been advanced.¹²

It could be that a small *average* advantage results from episodic times of intense population stress (e.g., after

meteor strikes, fire, flood, famine, climatic shifts, and the like) that could briefly impose nearly deterministic genetic selection (this is not the same as "punctuated equilibria," a view invoked mainly to explain long periods of apparent stasis). Or Darwin's assessment could have been wrong, and substantial advantages may arise more often than he thought, to be fixed so quickly that they are rarely around to be noticed. Selective coefficients could vary depending on allele frequency or ecological heterogeneity, but these ideas are usually offered to account for the maintenance of variation, not of small average selective coefficients (e.g.,^{9,12}).

There are other ways, perhaps. Much of evolution may occur not among competing organisms, but in the ability of gametes or germ-line cells simply to survive the chemical constraints of complex cellular life. Such constraints are probably deep and pervasive, but do not involve direct reproductive cost in the darwinian sense because organisms already so over-proliferate their gamete production (even human females produce millions of eggs) that this is more of an intrinsic than Malthusian constraint.

But even these ideas may be too conventional and too dependent on the desire for a darwinian solution, and there may be other ways to get ahead.

IS IT TRUE THAT MOST MUTATIONS ARE HARMFUL?

We can take a cue from Ohta's observation that even slightly *advantageous* alleles individually have only a small chance of actually becoming favored by nature. We routinely teach that after millions of generations organisms have become so highly organized by the directing force of selection that most new mutations introduce changes that put asunder what Nature hath joined together. That may not be true. Many or even most mutations—even functional mutations—may not be harmful after all.

From microbes to mammals organisms are proactive *exploratory* entities. Whether through chemistry or cognition, they use all sorts of environmental information from the chemical to the

ecological, to seek food, shelter, and mates, or avoid becoming prey, by finding favorable ways to live ("organismal" or "habitat" selection) or *creating* suitable environmental conditions where they can succeed ("niche construction").¹³⁻¹⁵ Behavior can sort organisms in functionally adaptive ways, but unlike natural or even sexual selection, behavioral sorting can be proactive rather than competitively defensive, and need not involve differential fitness. Athletes and anthropologists seek different fields but can coexist and have the same number of children. Because organisms sense best what they are able to do, behavior-based change can be faster than the relatively blunt and blind screen of selection, with more systematic, force-like effects that could generate the kind of reduced variation in the genes that enabled the sorting that is conventionally interpreted as natural selection.

For reasons mentioned earlier, non-disastrous alleles probably do not have an inherent selective effect (good or bad). Instead, a substantial fraction may constitute *opportunity* as much as detriment. In typical environments there may be hundreds of slightly different ways to make a living—to be "fit." Chance and exploratory behavior affect which path among these many equivalent viable paths is actually taken. Even if the effects are weak, since even without a selective push the probability of fixation is related to current frequency, a path once taken may be more likely to be followed even by chance alone. These kinds of mechanisms may help account for the speciose nature of many environments that contain numerous closely related and very similar cohabiting species, and may be especially likely to apply to primates, including our own hominine ancestors, for whom behavior is so central.

In light of these considerations, it is worth asking yourself: in which of these ways—or other ways—you think that the traits you are specifically interested in evolved?

ALL'S RIGHT THAT ENDS RIGHT

The vital aspect of Darwin's discovery was descent by natural processes from common ancestry, but a theory

can exercise a tight grip, and panselctionism came along for the ride. Panselctionism does not just weed out mistakes but also irresistibly favors “the smallest grain in the balance.” But while it is always *possible* that a variant will be detectable by selection, it is always *inevitable* that it will be affected by drift, and most if not all organisms are exploratory and facultative. A revised evolutionary landscape shows how random and behavioral effects may have a greater role in adaptation than usually thought—easing Darwin out of a fundamental error without undermining the idea of adaptation by natural means, if not always by natural selection.

Adaptation is a way to describe how organisms live. Once it becomes the normative “type” for a species, an adaptive trait almost automatically appears to have been specified by selection in a darwinian way.^{14,16} Population genetic models provide plausible, internally consistent descriptions of the long-term *net* result of evolutionary change. The increase in frequency of alleles useful to the present life-ways of organisms can be viewed *mathematically* in competitive (even deterministic) terms as having had some average selective advantage. In this sense, there are almost always enough millions of generations to bring about any observed gradual change, as Darwin thought (indeed, thousands usually suffice easily). The darwinian view also seems right that gradual rather than saltational change predominates in evolution. Darwinians should be happy.

But this does not mean the standard models explain what *actually* happened. Most who chance across this column

will probably hold more strongly selectionist views than I do. Even so, it is important to subject a strongly held view to scrutiny. For those who want to know how evolution has taken place on the ground, every day, among actual organisms, and how that is consistent with what we see today all around us, there is room for processes that involve genetic change but require less, and much less precise, selection, than Darwin and most biologists today invoke rather routinely. The behavior-based phenomena described above are wholly consistent with adaptive change, but do not require the kind of unrelenting selection Darwin thought was at work, need not involve much selection at all, and help us account for how very small selective variation might actually work, only less determinatively, more enabling rather than prescribing of some out of many possible tolerable options, than Darwin thought. These kinds of behaviors certainly happen in life, so there is room for alternative views.

After a century and a half of Darwin’s “long argument” as he calls the *Origin*, it turns out that everyone can be right (except Darwin?). If we adapt to a more realistic evolutionary landscape, we can remain “darwinian” in the most important senses of the term, without being trapped by the problems inherent in his Newtonian ideal. Because there are many ways for things that hardly matter at the time, to make all the difference in the end.

NOTES

I welcome comments on this column: kenweiss@psu.edu. I have a feedback page at http://www.anthro.psu.edu/weiss_lab/index.html. I thank Anne Buchanan, Sam Sholtis, and John

Fleagle for critically reading the manuscript. The Darwiniana quotes can be found in Carroll’s recent annotated reprint of the first edition of the *Origin*.¹⁷

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Many things discussed here can be profitably explored by web searching.

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ERRATUM

“Complementary Approaches of Cytogenetics and Molecular Biology to the Taxonomy and Study of Speciation Processes in Lemurs” by Ives Rumpler, Page 73, col. 1 states:

“. . . it clearly appears that *P. tattersalli* and *P. v. coronatus* cannot be classified in the same species.”

It should state:

“. . . it clearly appears that *P. tattersalli* and *P. v. conquerelli* cannot be classified in the same species.”